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UROSAURUS AND ITS PHYLOGENETIC RELATIONSHIP TO UTA AS DETERMINED BY OSTEOLOGY AND MYOLOGY (REPTILIA: IGUANIDAE)

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ABSTRACT.— The status of the genus *Urosaurus* Hallowell and its relationship to the genus *Uta* Baird and Girard as presented in previous studies are reviewed. Additional data from the head and throat osteology and myology are included in the analysis. Each bone and muscle is measured, ratios determined, and the position noted. Five distinct anatomical differences are noted between *Uta* and *Urosaurus*, and it is concluded that both of these genera are sufficiently different to warrant generic status. *Uta* is considered to be phylogenetically more primitive.

The climbing utas (*Urosaurus*) and the ground utas (*Uta*) are two genera which have had an uncertain systematic relationship. Studies by Mittleman (1942), Savage (1958), Etheridge (1962), and Larsen and Tanner (1975) have used various sets of morphological data to explain their affinities, but myological characteristics have been mostly neglected. Other studies involving taxonomy by Balanger and Tinkle (1973) and Tanner and Jorgensen (1963), ecology and external anatomy by Smith (1946), Tinkle (1967), Turner et al. (1970), and Tanner (1972), of *Uta* and *Urosaurus* and other related genera have been done. However, the validity of the genus *Urosaurus* and its position in the phylogeny of the Iguanidae has not been completely established. The present study is designed to investigate the anterior osteological and myological anatomy of these genera in order to determine their relationship to each other and to show their phylogenetic position in the family Iguanidae.

The literature dealing with the anatomy of iguanid lizards has been reviewed by Avery and Tanner (1971); therefore, we will confine our study primarily to problems relating to phylogeny. Data from previous studies, as indicated above, will be added to our myological findings.

Baird and Girard (1852) erected the genus *Uta* for the species *stansburiana*, which was characterized by gular folds, auricular openings, and a fine, homogeneous dorsal scalation. Later that year they described another form, *Uta ornata*, which differed from *stansburiana* in having the dorsal scalation composed of fine, strongly keeled, prominently imbricated scales which were divided into two parallel series on either side of the median dorsal line by a series of somewhat smaller, vertebral scales. However, Hallowell (1854) encountered a different lizard similar to *Uta ornata* Baird and Girard. It had enlarged dorsals extending the length of the dorsum in a broad and uninterrupted band and lacked the smaller, dividing series of scales. For this species Hallowell established the genus *Urosaurus*. Dumeril (1856) described the genus *Phymatolepsis* for a species similar to *Uta ornata* in that it has similar dorsals on either side of the smaller vertebral scales. These actions were challenged by Baird (1858) who described *Uta symmetrica*, a close relative of *Uta ornata*; and the next year he (Baird, 1859) placed Hallowell's *Urosaurus* in synonymy with *Uta* because of similar dorsal scalation and prominently characterized gular folds. *Urosaurus* was used as a subgenus by Van Den-

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burgh (1922). *Phymatolepsis* was placed in synonymy under *Uta* by Cope (1864). Although Fischer (1882) and Boulenger (1883) used the name, it was again placed in synonymy by Boulenger (1885).

Cope (1863) described the distinctive *Uta thalassina* from a general habitat sufficiently different from other known forms that Boulenger (1885) considered it generically distinct and proposed the name *Petrosaurus*. Boulenger's usage was ignored by Cope (1887), who retained *Uta thalassina*. Except for Van Denburgh (1922), who used *Petrosaurus* subgenerically, the name has been considered a synonym of *Uta*.

Mittleman (1942) reviewed the phylogenetic relationships of North American iguanid genera and considered *Ctenosaura* (Wiegmann, 1828) to have evolved from a primitive iguanid genus and to have given rise to two phyletic lines. The first contains *Crotaphytus* (Holbrook, 1842), and the other sceloporine line contains the following genera: *Uta* (Baird and Girard, 1852), *Urosaurus* (Hallowell, 1854), and *Sator* (Dickerson, 1919). *Uta* and *Urosaurus* are considered to have evolved from an early progenitor related to *Sceloporus*, which soon diversified sufficiently to produce *Uta* and *Urosaurus*. The latter genus is probably the older of the two. *Uta* probably did not disperse until the beginning of the Miocene, for it is restricted to the continental United States and Mexico and many of the adjoining islands. According to Mittleman (1942) *Uta* and *Urosaurus* "... may be considered as very nearly biological equivalents, for they are widely distributed, highly prolific, of about the same age, successful, and derived from closely related progenitors."

Sator (Dickerson, 1919), because of its relationship with *Sceloporus*, is also of interest. Although Dickerson (1919) mentioned certain osteological characteristics unique to *Sator*, the constant osteological variations within the genera *Sator*, *Sceloporus*, *Uta*, and *Urosaurus* have not been properly ascertained. Mittleman (1942) designates *Sator* as a direct derivative of the primitive *pyrocephalus* group of *Sceloporus* and considers it to be not closely related to any other lizard.

Stejneger and Barbour (1943) and Smith and Taylor (1950), in their checklist of lizards of the U.S. and Mexico,

adopted Mittleman's (1942) arrangement of the "utas," while Smith (1946) presented a somewhat modified phylogeny of North American iguanids that is, nevertheless, in basic agreement with Mittleman's work. Since Mittleman's study, herpetologists have been divided in their acceptance of his work as opposed to that of Oliver (1943), who did not recognize Mittleman's genera because he saw few characters separating them. Oliver retained all the species now assigned to either *Uta* or *Urosaurus* within the genus *Uta*. Schmidt (1953) and Stebbins (1954), among others, adhered to his view. Mittleman's classification was based upon his interpretation of external characteristics rather than upon marked structural differences between the several species groups.

Savage (1958) is in general agreement with Mittleman's two lines of phylogeny: the iguaine line and the sceloporine line. However, genera placed in the sceloporine line by the two authorities do not agree. Savage states that based upon the type of sternal arrangement there are two major subdivisions within the sceloporine group. Within the line having a utiform sternum, two distinct stocks are indicated. One of these is represented by the genus *Phrynosoma*, which lacks xiphisternal ribs. The other group, with the utiform sternum bearing xiphisternal ribs, contains the genera *Callisaurus*, *Holbrookia*, *Uma*, and *Uta*. Within *Uta*, the subgenus *Petrosaurus* is considered by Savage to be the most primitive, although highly adapted for a rock habitat. The genera *Urosaurus*, *Sator*, and *Sceloporus* are closely allied and differ from the other sceloporines in having a urosaurine type of sternum which possesses xiphisternal ribs. Thus in Savage's studies, based upon the type of sternal arrangements, *Uta* and *Urosaurus* are distinctly different genera.

Presch (1969) reports that the osteological characteristics indicate that the horned lizards (*Phrynosoma*) form a highly specialized genus within the *Sceloporus* group of genera (*Sceloporus*, *Sator*, *Uta*, *Urosaurus*, *Uma*, *Callisaurus*, *Holbrookia*, and *Petrosaurus*). *Phrynosoma* is distinguished from all other members of the family in having both a large sternal fontanelle and femoral pores. He lists *Petrosaurus* as primitive because of its moderately sized sternal fontanelle and

the presence of four sternal ribs. Of the two groups derived from *Petrosaurus*, the least altered are *Urosaurus*, *Uta*, *Sceloporus*, and *Sator*, which have hooks on the clavicle and a covering over the anterolateral processes of the frontal in some species, while *Holbrookia*, *Uma*, and *Callisaurus* are the most highly evolved. They have lost the lacrimal and postfrontal bones and the first pair of cervical ribs. Also, the interclavicle is shortened, and the anterolateral processes of the frontal are covered. Thus *Uta* and *Urosaurus* are placed in the same group but in distinctly different genera.

Etheridge (1964) claims that osteological comparisons do not provide a strong enough argument for or against the recognition of *Uta* and *Urosaurus* as separate genera. However, the few osteological differences between sceloporines that do exist suggest that three subgroups might be recognized: (1) *Holbrookia*, *Callisaurus*, and *Uma* with two cervical ribs (three in all others); (2) *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* with clavicular hooks present (absent in all others); and (3) *Petrosaurus* with four sternal ribs (two or three in others).

Hotton (1955) in his studies of dentition and food habits has implied that although *Uta* and *Urosaurus* are interpreted as direct but independent descendants of sceloporines, the dentition and diet of the *utas* are similar to *Callisaurus*. Lowe (1955) studied the problem of generic status of *Uta* and *Urosaurus* using ecological relationships. He was able to recognize genera on the basis of ecologic divergence alone, without the support of any other character.

On this ecological concept Lowe and Norris (1955) based their classification of the assemblage of lizards formerly placed in the genus *Uta*. They confirmed Mittleman's arrangement of these species because of supporting ecological differences between and similarities within the groups involved. As a result of their studies, they recognized the following taxonomic arrangement: genus *Petrosaurus* with subgenus *Streptosaurus*; genus *Uta* and genus *Urosaurus*.

Petrosaurus and *Streptosaurus* were placed together because of their cliff-dwelling habits. *Urosaurus* was retained as a distinct genus because the species within the group are plant dwellers and

climbers. *Uta* was distinguished from the other two genera by its ground-dwelling life-style.

Mittleman's classification of these iguanids has not been generally accepted by Savage and others because he failed to present convincing evidence that the several groups were morphologically different from one another. The most striking morphological feature listed by Mittleman as separating *Uta* from *Urosaurus* was the homogeneous scutellation of the former and the differentiation of the paravertebral scales in the latter.

We extend our gratitude to those who have helped us in the preparation of this paper. We are grateful to Dr. Ernest Williams, at the Department of Herpetology, Museum of Comparative Zoology at Harvard, for providing us with various prepared skeletons of *Uta* and *Urosaurus*. We also thank Mr. Chester J. Bosworth and Dr. Dwight G. Smith, who have been so kind as to read and criticize this study, distribute necessary literature, and make suggestions. We are grateful to Kenneth R. Larsen and Wilmer W. Tanner for making available a copy of the manuscript of Larsen and Tanner (1975). Lastly we thank Southern Connecticut State College for financial aid and the loan of materials and space for part of this study, and Brigham Young University for editorial and publication courtesies.

MATERIALS AND METHODS

Skeletons used in the study were borrowed from the Museum of Comparative Zoology at Harvard (MCZ), and preserved specimens were borrowed from Southern Connecticut State College (SCSC).

One skeleton of *Urosaurus ornata wrighti* and three of *Uta s. stansburiana* were prepared by carefully stripping away the skin, connective fascia, and large muscle the first day of skeletonizing. After drying, the remaining tissues were removed by stripping and picking until the skeletons were clean.

All measurements were taken in millimeters with an ocular micrometer mounted in a dissecting microscope. All measurements were taken from the extreme points of the width and length of each structure.

Specimens are accessioned in the natural history collection of MCZ and/or

SCSC. The materials utilized for this study are as follows:

Osteology

Uta stansburiana stansburiana Baird and Girard

MCZ 62443, Utah

SCSC 381, East of Elberta, Utah

SCSC 382, East of Elberta, Utah

SCSC 383, East of Elberta, Utah

Urosaurus ornata symmetrica (Baird)

MCZ 26695, Fort Yuma, Arizona

Urosaurus ornata linearis (Baird)

MCZ 04947, Tucson Mt. Park, Arizona

Urosaurus ornata lateralis (Boulenger)

MCZ 14345, Guaymas, Mexico

Urosaurus ornata schotti (Baird)

MCZ 64122, Sonora, Southern Guaymas,

Mexico

Urosaurus ornata wrighti Schmidt

SCSC 384, Moab, Utah

Myology

Uta stansburiana stansburiana Baird and Girard

SCSC 381, Utah County, Utah

SCSC 382, Utah County, Utah

SCSC 383, Utah County, Utah

Urosaurus ornata (Baird)

SCSC 921, Moab, Utah

SCSC 922, Moab, Utah

SCSC 923, Moab, Utah

OSTEOLOGY

A study of the osseous elements of *Uta* and *Urosaurus* reveals a basic pattern that was described by Savage (1958), Ethridge (1964), and Avery and Tanner (1971) for these and other iguanids. As a result we confine our descriptions to deviations from that pattern.

Skull and Jaws

An analysis of the skull and jaw was made from data obtained by examining their size and shape. After skulls were measured, a percentage was computed between length and width and compared with similar data for both genera. Measurements and ratios were taken for identical bones in both genera. Those bones having an average mean greater than 40 points are presented in Tables 1 and 2.venience of reference the skull has been subdivided into a posterior occipital unit and an anterior maxillary unit.

The skulls are streptostylic with a freely movable quadrate bone which ar-

TABLE 1.— Minimum, mean, and maximum measurements and ratios for the skull structures of *Uta*.

Name of structure	Length		Width		Width-length ratio	
	Min.	Mean	Max.	Min.	Mean	Max.
Basisphenoid	1.22	1.35	1.46	1.71	1.83	1.95
Basioccipital	1.46	1.75	2.14	2.20	2.46	2.78
Pterygoid	3.95	4.58	5.12	1.27	1.62	2.30
Ectopterygoid	2.20	2.26	2.44	1.61	1.77	1.95
Vomer	1.76	1.92	2.04	.780	.830	.880
Palatine	1.71	1.92	2.10	.975	1.18	1.22
Premaxilla	1.42	1.86	2.43	1.46	1.67	2.24
Maxilla	4.78	5.08	5.50	1.95	1.99	2.04
Nasal	1.80	1.97	2.04	.486	.658	.975
Prefrontal	2.39	2.62	2.88	.490	1.41	1.90
Lacrimal	.487	.573	.684	.390	.573	.732
Frontal	3.90	4.07	4.35	3.66	4.02	4.64
Postorbital	1.07	1.92	2.62	1.66	1.79	1.95
Jugal	6.10	6.58	7.22	.440	.610	.732
Parietal	3.24	3.86	4.10	5.15	5.66	5.90
Postfrontal	.487	.682	.926	.098	.195	.293
Squamosal	2.30	2.60	2.93	.685	.841	1.07
Quadrate	.735	.811	.975	1.95	2.32	2.44
Supratemp. Fossa	2.78	2.91	3.01	1.12	1.36	1.51
Orbit	4.35	4.41	4.50	3.17	3.37	3.47
Nasal Opening	.975	1.38	1.61	1.02	1.15	1.42
Dentary	6.60	7.08	7.80	.972	1.15	1.22
Articular	3.16	3.46	3.86	.586	.720	.880
Angular Pr.	5.70	6.89	9.50	4.77	6.07	7.15
Surangular	2.20	3.17	4.13	.440	.598	.780
Splenial	2.20	2.42	2.58	.195	.242	.585
Angular	5.70	6.89	9.50	1.43	1.88	2.30
Coronoid	2.20	3.23	4.40	1.46	1.67	2.04
Pyriform Recess	2.68	3.17	3.42	2.04	2.27	2.44
Parasphenoid Pr.	.925	1.21	1.46	.487	.487	.487
Entire Skull	11.2	11.6	11.9	6.35	7.26	8.05

TABLE 2.— Minimum, mean, and maximum measurements and ratios for the skull structures of *Urosaurus*.

Name of structure	Length			Width			Width-length ratio		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
Basisphenoid	1.56	1.71	1.95	1.90	2.01	2.14	.800	.872	1.00
Basioccipital	1.22	1.57	1.80	2.68	2.89	3.17	.455	.555	.675
Pterygoid	4.00	4.74	5.37	1.17	1.32	1.46	.280	.304	.366
Ectopterygoid	1.41	1.84	2.24	1.17	1.50	1.80	.655	.753	.880
Vomer	1.22	1.76	2.44	.733	.811	.930	.340	.488	.680
Palatine	1.46	1.84	2.20	.975	1.24	1.71	.445	.848	1.00
Premaxilla	1.22	1.44	1.56	1.71	2.23	2.58	.565	.656	.730
Maxilla	5.26	5.84	6.10	2.20	2.21	2.34	.360	.405	.437
Nasal	2.04	2.32	2.78	.830	.946	1.07	.360	.410	.464
Prefrontal	2.74	2.91	3.12	1.07	1.22	1.36	.344	.419	.462
Lacrimal487	.615	.737	.487	.615	.732	.073	.286	1.00
Frontal	3.80	4.15	4.40	4.40	4.60	4.87	.780	.902	.990
Postorbital	2.44	2.75	3.18	1.71	1.86	1.95	.538	.688	.800
Jugal	5.37	6.00	6.35	.540	.635	.732	.088	.106	.127
Parietal	3.90	4.08	4.30	5.35	5.64	5.96	.661	.723	.765
Postfrontal585	.791	.975	.024	.190	.440	.024	.255	.500
Squamosal	2.44	2.55	2.93	.780	.940	1.07	.327	.370	.440
Quadrate930	1.07	1.32	2.20	2.34	2.64	.405	.460	.590
Supratemp. Fossa	2.78	3.14	3.36	1.32	1.54	1.76	.430	.448	.525
Orbit	3.90	4.59	4.90	3.42	3.68	3.90	.720	.806	.875
Nasal Opening	1.49	1.52	1.61	.585	.975	1.22	.388	.656	.897
Dentary	6.84	7.15	7.60	.810	.889	.928	.118	.124	.131
Articular	3.26	3.44	3.76	.974	1.39	1.85	.300	.399	.507
Angular Pr.	5.70	6.30	7.15	5.70	6.77	8.10	.705	.875	1.00
Surangular	2.68	2.86	3.26	.684	.794	.880	.225	.271	.328
Splenial	2.20	2.53	2.92	.244	.478	.585	.084	.156	.244
Angular	5.70	6.30	7.15	1.43	1.03	1.90	.252	.284	.333
Coronoid	2.68	2.96	3.18	1.27	1.73	1.95	.400	.591	.726
Pyriform Recess	2.44	2.76	3.18	1.76	2.08	2.44	.635	.760	.910
Parasphenoid Pr.925	1.25	1.42	.440	.597	.925	.360	.474	.650
Entire Skull	11.2	11.6	12.4	6.75	7.38	7.80	.582	.633	.670

ticulates dorsally with the paroccipital process and ventrally with the quadrate process of the pterygoid. Thus, they form a compact, light, and strong cage for the brain and sense organs.

The actual shape of the skull is either elongated and flattened dorsoventrally, as in *Uta*, or shortened and laterally compressed, as in *Urosaurus*. Measurements of the length of the skull were from the top of the premaxillary bone to the most posterior extension of the occipital condyle. Measurements of the width were from the widest extension between the sub-orbital bars in the area of the orbit.

The means in Tables 1 and 2 indicate that *Uta* has a slightly lower skull ratio (.623) than *Urosaurus* (.633). For con-

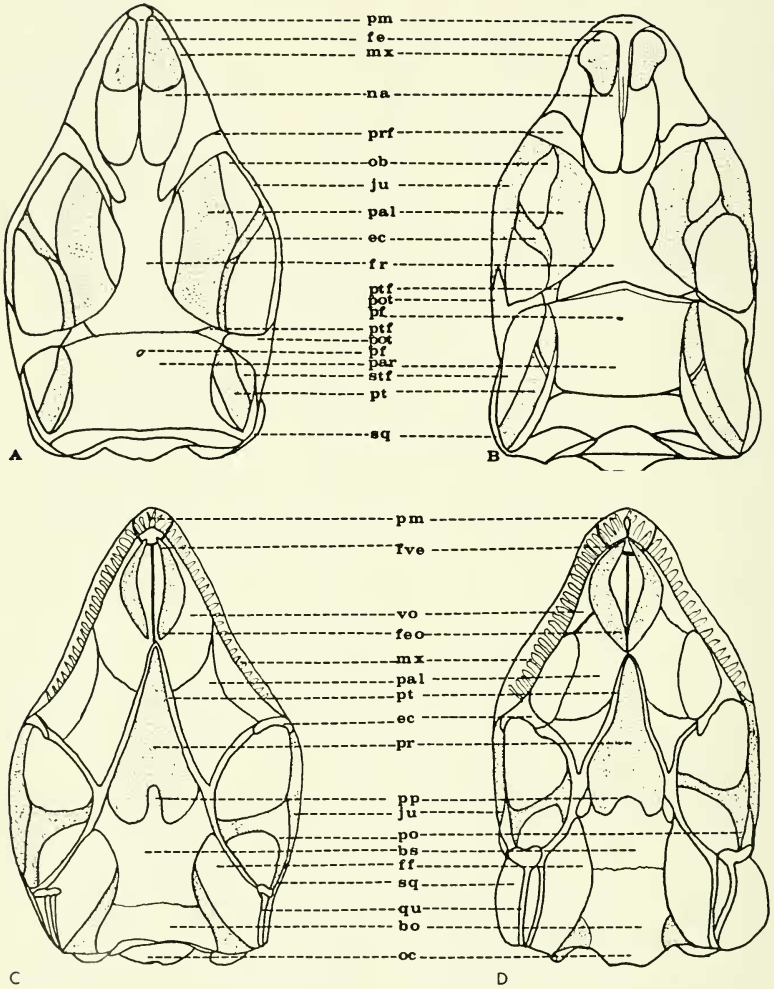
The occipital portion forms a median wall for the attachment of the neck and articulation for the remainder of the skull. It consists of two parts: (a) braincase (basisphenoid, basioccipital, prootic, exoccipital, supraoccipital) (b) foramen magnum (enclosed by the basioccipital, exoccipitals, and supraoccipital). A tripartite occipital condyle is located on the pos-

terior end of the basioccipital and the lateral exoccipital in all iguanine genera.

Basisphenoid: Length is from the suture between basisphenoid and basioccipital, to the beginning of the parasphenoid process (Fig. 1). Width is the distance between the widest expansion of the basiop-terygoid processes. The lowest ratio mean is in *Uta* (.767), the highest in *Urosaurus* (.872). A low ratio indicates that the bone is much longer than it is wide, whereas the higher ratios indicate bones with lengths and widths more nearly equal.

Basioccipital: Length is from the suture between the basisphenoid and basioccipital to the posterior tip of the occipital condyle (Fig. 1); and width is between the tips of the lateral extensions of the sphenoccipital tubercles. The ratio in *Uta* is .701 and *Urosaurus* .555.

Pterygoid: Length (Figs. 1, 2, 3) is between the anterior portion of the pterygoid where it sutures with the palatine and the most posterior tip of the quadrate process. Width is between the articulation with the basiptyergoid process of the basisphen-

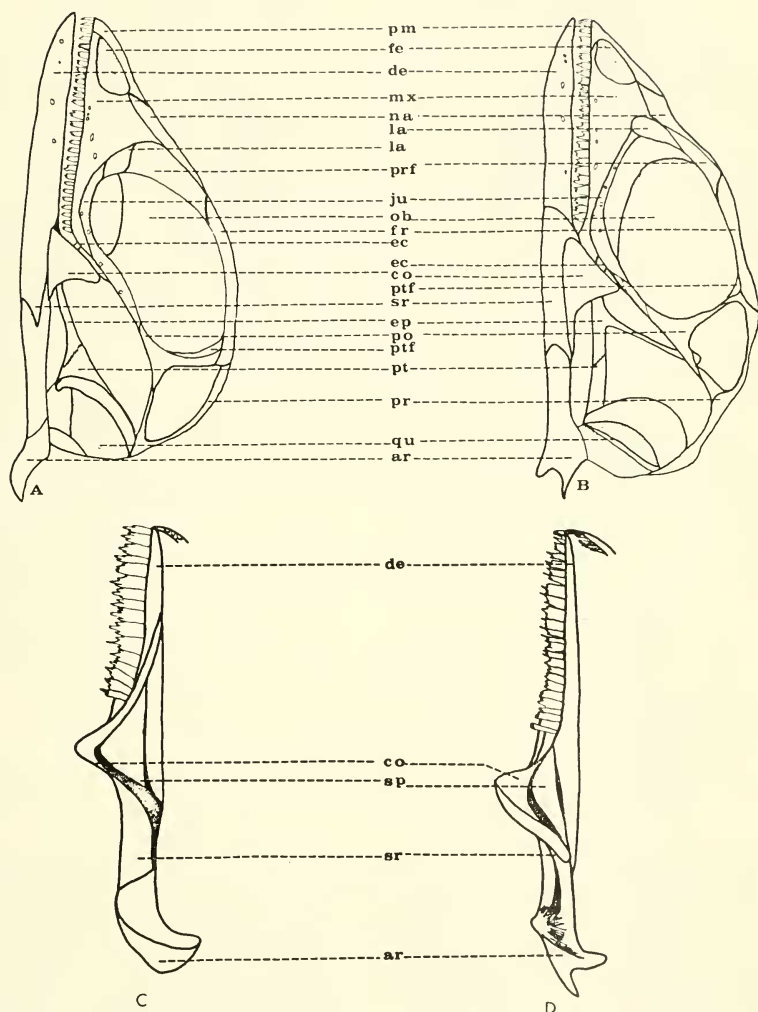


BO—Basioccipital
BS—Basisphenoid
EC—Ectopterygoid
FE—Fenestra exonarina
FEO—Fenestra exochoanalis
FR—Frontal
FVE—Fenestra vomer-
onassalis externa
JU—Jugal

MX—Maxilla
NA—Nasal
OB—Orbit
PAL—Palatine
PAR—Parietal
PF—Pineal foramen
PM—Premaxilla
POT—Postorbital
PP—Parasphenoid process

PR—Pyriform recess
PRF—Prefrontal
PT—Pterygoid
PTF—Postfrontal
QU—Quadrate
STF—Supratemporal fossa
SQ—Squamosal
VO—Vomer

Fig. 1. Dorsal and ventral views of skulls. A and C *Uta*, B and D *Urosaurus*.

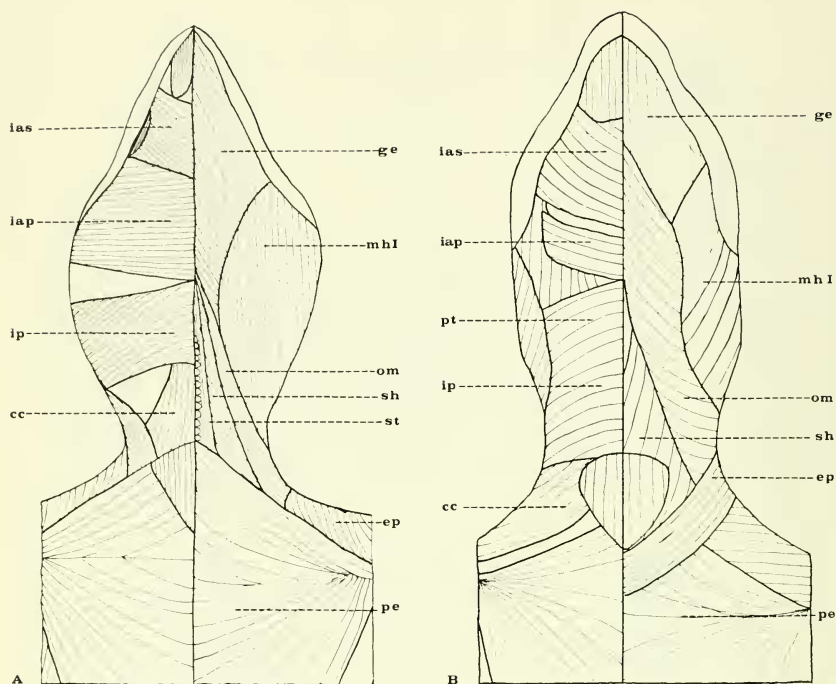


AR—Articular
CO—Coronoid
DE—Dentary
EC—Ectopterygoid
EP—Epipterygoid
FE—Fenestra exonarina
FR—Frontal

JU—Jugal
LA—Lacrima
MX—Maxilla
NA—Nasal
OB—Orbit
PM—Premaxilla
PO—Postorbital

PRF—Prefrontal
PR—Parietal
PT—Pterygoid
PTF—Postfrontal
QU—Quadrate
SP—Splenia
SR—Surangular

Fig. 2. Lateral view of skull and medial view of mandible. A and C *Uta*, B and D *Urosaurus*.



CC—Constrictor colli
EP—Episternocleidomastoideus
GE—Genioglossus
IAP—Intermandibularis
anterior profundus

IAS—Intermandibularis an-
terior superficialis
NP—Intermandibularis pos-
terior
MHI—Mandibulohyoideus I

OM—Omohyoideus
PE—Pectoralis
SH—Sternohyoideus
ST—Sternothyroideus

Fig. 3. Ventral view of throat musculature; superficial depth at left and first depth at right. A. *Uta*; B. *Urosaurus*.

oid and the suture with the ectopterygoid. The ratio is *Urosaurus* .304 and *Uta* .354.

Ectopterygoid: Length (Figs. 1, 2) is between the suture with the pterygoid and the suture with the jugal and maxilla. The greatest diameter is at its point of union with the jugal and maxilla. The lower ratio is in *Uta* (.704) and the higher in *Urosaurus* (.753).

Vomers: Length (Fig. 1) is from the anterior suture with the premaxilla to the most posterior point of the suture with the palatine. Width is between the median border of the vomer at the ventral midline and the most lateral border where it attaches to the maxilla. The ratio in *Urosaurus* is .488 and in *Uta* .431. The vomers possess a small blunt projection

which protrudes from its lateral border into the opening of the fenestra excho-analis and fenestra vomeronasalis externa and divides the opening. This anterolateral projection is seen in both genera.

Palatine: Length is from the anterior suture with the vomer at the midline to the most posterior extension of the suture with the pterygoid (Fig. 1). Width is from the skull's midline to the lateral suture between the palatine and the maxilla. The ratio in *Urosaurus* is .848 and in *Uta* .579.

Premaxillae: Length (Figs. 1, 2) is from its anteroventral tip to its dorsal union with the nasal at the dorsal midline. Width is between the lateral sutures shared by the premaxillae with the maxil-

la on the ventral surface of the premaxilla. The ratio in *Uta* is .733 and in *Urosaurus* .656.

Maxillae: Length (Figs. 1, 2) is from the most anterior extension of the premaxillary process to the posterior-most extension of the maxillae where it sutured with the jugal and ectopterygoid. Width is the vertical distance from the ventral border of the maxillae to the dorsal-most extension at the point of suture with the nasals and prefrontals. The ratio in *Uta* is 3.96 and in *Urosaurus* .405.

Nasal: Length (Figs. 1, 2) is from the tip of the ventral border as it forms the fenestra exonarina to the posterodorsal extension that sutures with the prefrontal. Width is from its medial suture with its opposite member to its most lateral extension where it sutured with the maxilla and prefrontals. The ratio in *Urosaurus* is .410 and in *Uta* .332.

Prefrontal: Length (Fig. 1) is from the suture between the prefrontal and lacrimal bones at the anterior lip of the orbit, to the suture between the prefrontal and frontal. Width is from the suture between the prefrontal and lacrimals to the median point where the frontal, nasal, and prefrontal bones suture together. The ratio in *Uta* is .433 and in *Urosaurus* .419.

Lacrimal: Length is from the antero-dorsal border as it sutures with the prefrontal and maxilla to the posterior border on the rim of the orbit as it sutures with the jugal (Fig. 2). Width is the distance between the dorsal border of the lacrimal at the rim of the orbit to its ventral border at its suture with the maxilla. The ratio in *Uta* is .101 and in *Urosaurus* .286.

Frontal: Length (Figs. 1, 2) is from the most anteromedian suture shared with the parietal. Width is between the most lateral posterior projections which suture with the parietal and postfrontal. The ratio in *Uta* is .903 and in *Urosaurus* .902.

Postfrontal: Length (Figs. 1, 2) is the extremities of its longest axis. Width is the distance between the parallel borders on the axis at right angles to the length. The ratio in *Urosaurus* is .255 and in *Uta* .288.

Jugal: Length (Figs. 1, 2) is between its most anterior projections as it sutures with the lacrimal and maxillae, to the posterior projection which sutures to the anteroventral border of the postorbital. Width is the distance between the two

parallel borders at right angles to the length. The ratio in *Uta* is .092 and in *Urosaurus* .106.

Parietal: Two measurements (Figs. 1, 2) were taken. The anterior two-thirds of the bone was subjected to length-width measurements, with the length being the distance along the midline, from the anterior suture with the frontal to the suture between the parietal and the supraoccipital. Width is the distance between the two anterolateral projections that suture with the postorbital and postfrontal. The ratio in *Urosaurus* is .723 and in *Uta* .680.

Postorbital: Length (Figs. 1, 2) is between the anteroventral and postventral projections. Width is from the ventral border to the tip of the dorsal projection where it sutures with the parietal and postfrontal bones. The ratio in *Uta* is .711 and in *Urosaurus* .688.

Squamosal: Length (Fig. 1) is between the most anterior and posterior extremities. Width is between the parallel borders on an axis at right angles to the length. Ratio in *Urosaurus* is .370 and in *Uta* .325.

Quadrato: Length (Fig. 2) is from its dorsal border where it attaches to the squamosal and the ventral extremity of the condyle which articulates with the articular. Width is between its medial and lateral borders. The ratio in *Urosaurus* is .460 and in *Uta* .346.

Supratemporal fossa: Its length (Fig. 1) is the inside distance on the longest axis and width the inside distance on the longest axis at right angles to the length. The ratio in *Uta* is .467 and in *Urosaurus* .488.

Orbit: Length (Figs. 1, 2) is between the lacrimal and postorbital. Width is between jugal and frontal bones. The ratio (most circular opening) in *Urosaurus* is .806 and (most elliptical opening) in *Uta* .762.

Fenestra exonarina: Length (Fig. 1) is the internal distance between the lateral projection of the premaxilla and maxilla and the suture between the nasal and maxilla. Width is the inside distance between the lateral border of the premaxilla and the anterior border of the maxilla. The ratio (most circular opening) in *Uta* is .770 and (most elliptical opening) in *Urosaurus* .656.

The lower jaw consists of two paired rami united anteriorly in a mental symphysis. Each articulates posteriorly with

the quadrate. The dentary of each ramus bears a single row of pleurodont teeth, whereas the remaining bones (articular, surangular, angular, splenial, and coronoid) are edentate.

Dentary: Length is from the anterior tip to the posterior-most projection on the lateral surface of the mandible (Fig. 2). Width is the vertical distance between the top and the bottom of the mandible, immediately in front of the coronoid. The ratio in *Uta* is .163 and in *Urosaurus* .124.

Articular: Length (Fig. 2) is from its most anterior projection on the median surface where it sutured to the coronoid and splenial to the most posterior tip of the retroarticular process. Width is from the most ventromedial projection of the angular process to the opposite border of the articular where it sutured with the surangular on the lateral surface. The ratio in *Urosaurus* is .399 and in *Uta* .207.

The angular process of the articular bone differs in shape and size in each genus. This projection was also subjected to length-width measurements. The length is the greatest length of the mandible and was contrasted with the width of the articular, which in part is a result of the size of the angular process. *Urosaurus* .875 has the greatest ratio (shortest, widest) while the smallest (longest, narrowest) is in *Uta* .824.

Surangular: Length is the longest anterior-posterior axis on the lateral surface of the mandible (Fig. 2). Width is the longest dorsal-ventral axis in the area of the anterior sutures with the dentary and coronoid on the lateral surface. The ratio (shortest, widest) is in *Urosaurus* .271 and in *Uta* .185.

Splenial: Length is the longest anterior-posterior axis and the greater dorsal-ventral axis is the width. The ratio (shortest, widest) is in *Uta* .174 and in *Urosaurus* .156.

Angular: The angular is roughly fusiform; its length is between the most anterior and most posterior projections. Width is between the opposite borders on an axis at right angles to the length. The ratio (shortest, widest) in *Urosaurus* is .284 and in *Uta* .280.

Coronoid: Length is from the dorsal tip of the bone to the tip of the ventral-most projection on the lateral surface (Fig. 2). Width is between anterior

and posterior borders where they contact the dorsolateral surface of the mandible. The ratio in *Urosaurus* is .591 and in *Uta* .560.

MYOLOGY

To avoid confusion, the terminology used for the following descriptions of the muscles is that of Robison and Tanner (1962), Jenkins and Tanner (1968), and Avery and Tanner (1954, 1971). The musculature also follows the basic iguanid pattern described by the above. Only deviations will be noted in the text.

Throat Musculature

M. Intermandibularis anterior superficialis is constant in both genera examined with the following exception; slightly broader in *Urosaurus* than *Uta* (Fig. 3). However, in both genera the muscle is sheetlike with the width at least half the length.

M. Intermandibularis anterior profundus is relatively consistent in its location; however, in *Uta* it is a wide band of muscle attached to the intermandibularis anterior superficialis. In *Urosaurus* it is a thin sheet separated anteriorly from the intermandibularis anterior superficialis and posteriorly from the intermandibularis posterior by a thin membrane (Fig. 3).

M. Intermandibularis posterior is continuous posteriorly with the constrictor colli from which it can be delineated by a natural separation of the muscle fiber bundles (Figs. 3, 9 and 10). The possession of this separation is varied in the genera examined. In *Urosaurus* the constrictor colli and intermandibularis posterior are closely associated along their entire common border. In *Uta* the two muscles are separated totally laterally but are continuous for a short distance near the midline raphe.

M. Mandibulohyoideus I in *Urosaurus* has approximately one-half of its body covered by the omohyoideus, whereas in the *Uta* only a small posterior portion is covered (Fig. 3).

M. Mandibulohyoideus II was described by Avery and Tanner (1971) for other iguanids. However, we were unable to locate this muscle in either *Uta* or *Urosaurus*.

M. Mandibulohyoideus III in both *Uta* and *Urosaurus* arises from the ventro-

medial surfaces of the dentary and angular between the anterior and posterior myoloid foramina (Fig. 4). The narrow insertion is on the lateral surface of the ceratohyal distal to its midpoint.

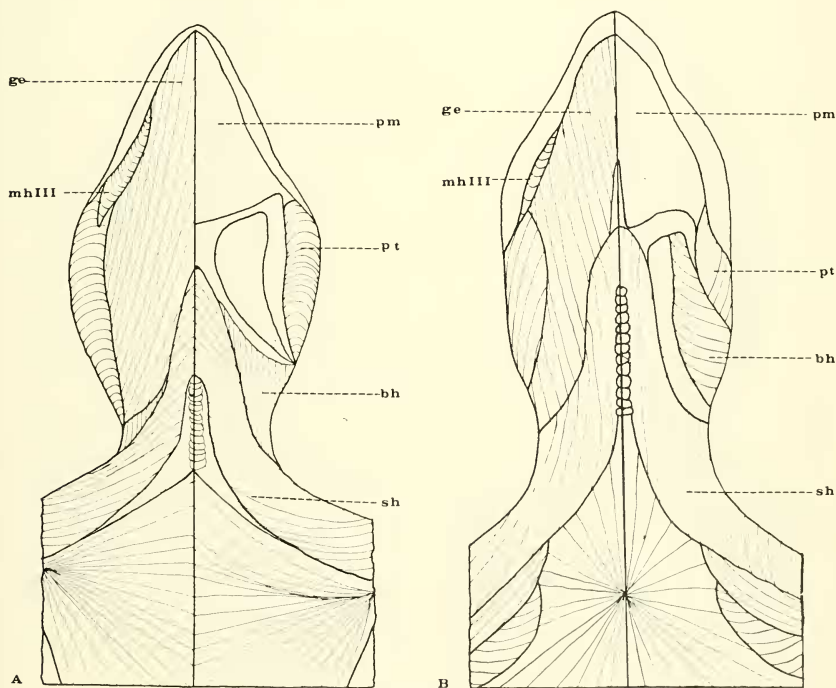
M. Genioglossus is a thick bandlike muscle in both genera which occupies a large area between the mandibular rami (Figs. 3 and 4). Its position is ventral to the tongue and anterior to the basihyal. The first, second, and third mandibulohyoideus and the intermandibularis muscles are all dorsal to it.

M. Hyoglossus is as described in other iguanids.

M. Branchiohyoideus in *Uta* (as in *Sauromalus*) has a narrow insertion on the first ceratobranchial, whereas in *Urosaurus* the insertion covers over half the distal

portion of the first ceratobranchial (Fig. 4).

M. sternohyoideus, as reported in the literature, is subject to considerable confusion concerning its limits (Figs. 3, 4, 6). Davis (1934:19) considers the superficial layer to be divisible into three parts in *Crotaphytus*. One of these muscles he calls the omohyoideus. Robison and Tanner (1962:6) consider this muscle continuous in the same genus. Oelrich (1956:51-52) treats this muscle in *Ctenosaura* as being continuous, but owing to the different origin and direction of the fibers he separates the layers into omohyoideus and sternohyoideus. Kesteven (1944:245-246) studied the agamid, *Phrynosoma*, suggesting a separation in young specimens and treats these layers as con-



BH—Branchiohyoideus
GE—Genioglossus

MHIII—Mandibulohyoideus III
PM—Pharyngeal membrane

PT—Pterygoidmandibularis
SH—Sternohyoideus

Fig. 4. Ventral view of throat musculature; second depth at left and third depth at right. A. *Uta*; B. *Urosaurus*.

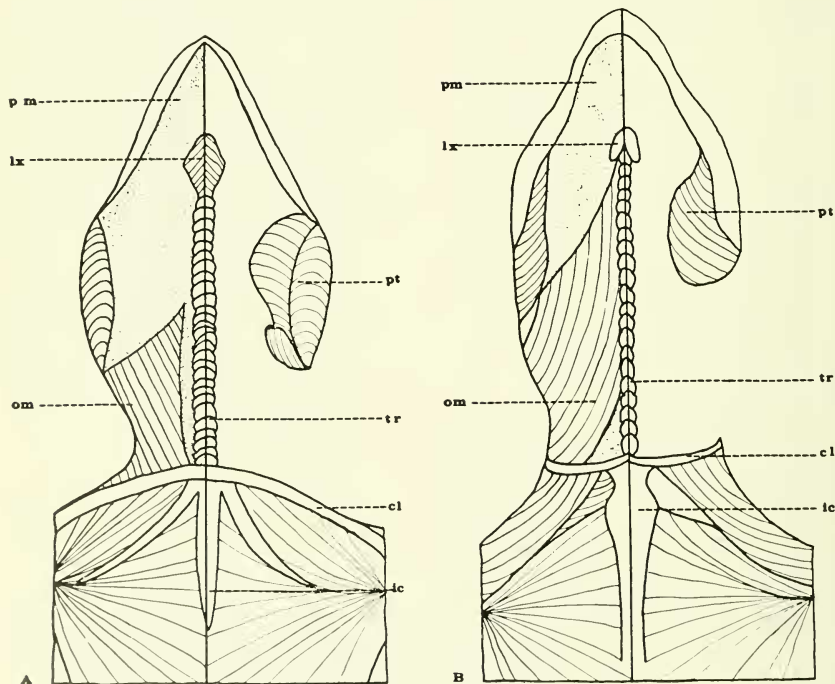
sisting of three parts which he considers to represent the similar, though distinct, divisions present in *Varanus*. In the iguanines Avery and Tanner (1971) treated the sternohyoideus complex as three separate muscles, sternohyoideus, sternothyroideus, and omohyoideus. This arrangement is followed here. In both genera examined, the sternohyoideus forms a broad elongated sheet of muscle covering the posterior portion of the mandibulohyoideus I muscle.

M. omohyoideus is sheetlike and forms the lateral extension of the sternohyoideus complex (Figs. 3, 5, 10). In both genera it originates medially from the lateral tip of the transverse process of the interclavicle with some fibers of the episternocleidomastodeus. Laterally, the omohyoideus

originates from the anterolateral surface of the clavicle and anterior border of the suprascapula. Its fibers pass obliquely anterior to insert on the posterior margin of the first ceratobranchial and the proximal end of the second ceratobranchial cartilages.

In both genera the median border is separated from the lateral border of the sternohyoideus. The delineation of both muscles must be made by comparing the origins and insertions. In *Urosaurus* it is easily separated, as the fibers of this muscle pass oblique to those of the sternohyoideus covering most of the mandibulohyoideus I. In *Uta* it is a thin band just lateral to the sternohyoideus.

M. Sternothyroideus is the most medial extension of the sternohyoideus complex



CL Clavicle
IC Interclavicle
LX Larynx

OM Omohyoideus
PM Pharyngeal membrane
PT Pterygoideomandibularis

TR Trachea

Fig. 5. Ventral view of throat musculature; fourth depth at left and fifth depth at right. A. *Uta*; B. *Urosaurus*.

and can be separated from the other members of the group by its different origin and insertion (Fig. 3). The name sternothyroideus is used as in Camp (1923: 451), who figured it as the deep member of the complex in *Brachylophus*.

The origin is considered to be those fibers arising from the interclavicle and sternum. These fibers pass anteriorly and parallel to the trachea to insert on the hyoid at the point of union between the basihyoid and hypohyal.

In *Urosaurus* the lateral border of the sternothyroideus and the median border of the sternohyoideus are difficult to determine. In *Uta* their separation is distinguishable since the three muscles have fibers oblique to one another as described for *Sauromalus* by Avery and Tanner (1971).

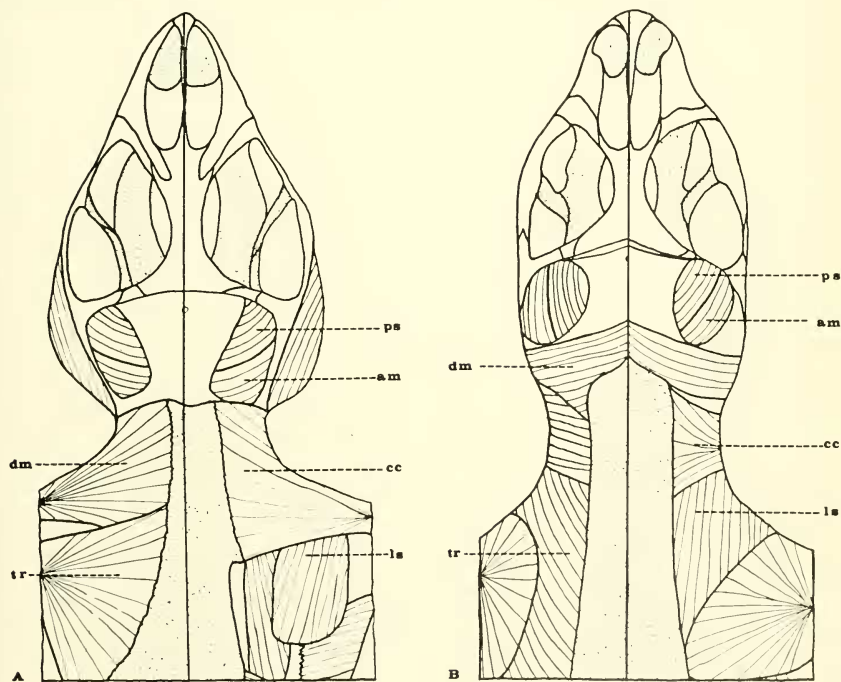
Neck Musculature

M. Constrictor colli is variable in width in both genera (Figs. 3, 4, 9). It is widest, covering most of the lateral surface of the neck, in *Urosaurus*. A narrow constrictor colli occurs in *Uta*.

M. Episternocleidomastoideus was found as a thin band of muscle extending over the shoulder in *Uta*, whereas in *Urosaurus* it is at a greater depth (Figs. 3, 7, 9, 10, and 11).

M. Depressor mandibularis (Figs. 6, 9, 10) is divided into three bundles as described by Avery and Tanner (1971). The third bundle (cervicomandibularis) in *Uta* and *Urosaurus* is completely obscured by the more superficial constrictor colli.

M. Levator scapulae superficialis is not



AM—Adductor mandibularis
externus medius
CC—Constrictor colli

DM—Depressor mandibularis
LS—Levator scapulae
superficialis

PS—Pseudotemporalis
superficialis
TR—Trapezius

Fig. 6. Dorsal view of head and neck musculature: superficial depth at left and first depth at right. A. *Uta*; B. *Urosaurus*.

as fan shaped in *Uta* as in *Urosaurus* (Figs. 6, 7, 10, 11, and 12).

M. Levator scapulae profundus has a more superficial position in *Uta* than in *Urosaurus* (Figs. 7, 12).

Temporal Musculature

M. Pterygomandibularis does not deviate from the typical iguanid pattern (Figs. 4, 5).

M. Levator angularis oris differs in size in *Urosaurus* where it covers over half the intratemporal fossa (Fig. 9). In *Uta* it is narrower, covering approximately one-third of the fossa.

M. Adductor mandibularis externus superficialis is similar to that of other iguanids (Figs. 9, 10).

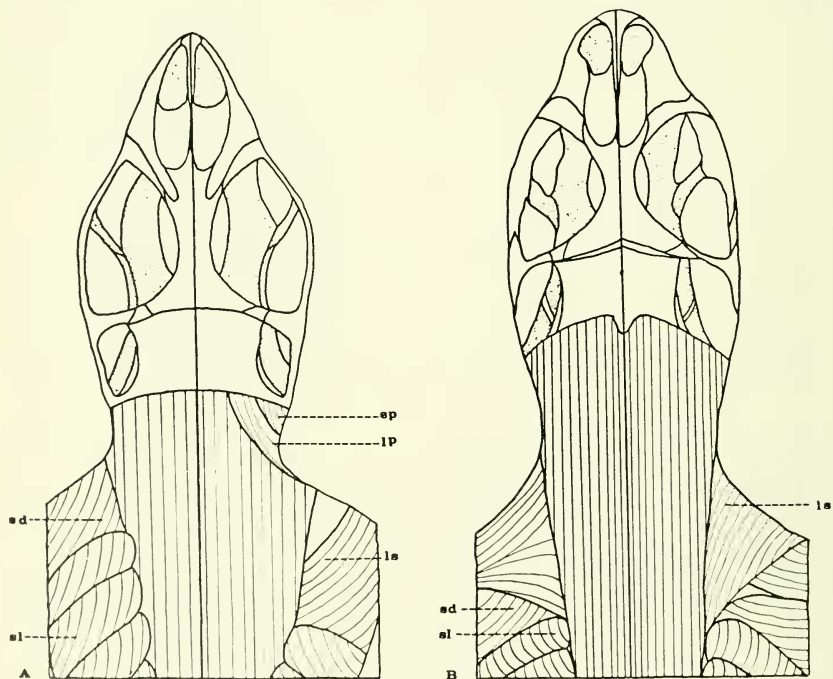
M. Adductor mandibularis externus medius is also with the typical iguanid pattern (Figs. 6, 9, 10, 11).

M. Adductor mandibularis externus profundus is as in other iguanids (Fig. 12).

M. Pseudotemporalis superficialis does not deviate from other iguanids (Figs. 6, 12).

M. Pseudotemporalis profundus is more obscured by the levator pterygoideus in *Urosaurus* than in *Uta* (Fig. 13).

M. Adductor mandibularis posterior shows some variations in the two genera, particularly in the location of the muscle with reference to the auditory meatus (Fig. 13). In *Urosaurus* it is located both ventral and anterior to the meatus, whereas in *Uta* the muscle is found slightly ventral to the meatus.



EP—Episternocleidomastoideus LS—Levator scapulae
LP—Levator scapulae profundus superficialis

SD—Serratus (dorsal part)
SL—Sacrolumbalis

Fig. 7. Dorsal view of head and neck musculature; second depth at left and third depth at right. A. *Uta*; B. *Urosaurus*.

M. Levator pterygoideus is as seen in other iguanids (Fig. 14).

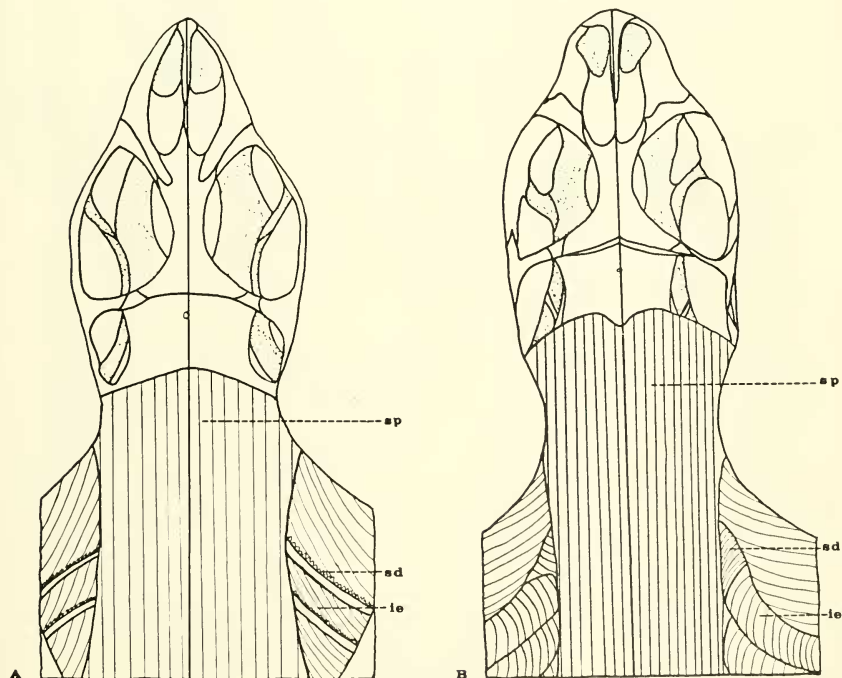
M. Protractor pterygoideus has a much larger insertion on the medial crest of the quadrate in *Urosaurus* than in *Uta* (Figs. 13, 14).

DISCUSSION

A study of the anterior osteology and myology of *Uta* and *Urosaurus* reveals some distinct anatomical differences between the two genera.

Mittleman (1942) considered the relationship between *Uta*, *Urosaurus*, and the iguanines (*Sauromalus*, *Dipsosaurus*, and *Ctenosaura*). He regarded *Uta* and *Urosaurus* as distinct genera. Savage (1958) outlined the iguanine characteristics and included *Crotaphytus* in that evolutionary line. He also determined some structural differences between *Uta* and *Urosaurus*. The differences cited by Savage include

Urosaurus possessing a pectoral girdle of the urosaurine type: lateral xiphisternal ribs present and no supranasal scales. *Uta* is distinctly different in having a pectoral girdle of the utiform type, no lateral xiphisternal ribs, and supranasal scales separating nasals from internasals. Avery and Tanner (1964) present several myological differences between *Sauromalus* and *Crotaphytus* and indicate these two genera are not in the same evolutionary line, indicating that at least two major subdivisions exist in the family Iguanidae. Etheridge, in 1964, also examined the iguanines and separated *Crotaphytus* from them based on osteological differences. He states that three subgroups of sceloporines may exist: (1) *Holbrookia*, *Callisaurus*, and *Uma* possessing the scapular fenestra; (2) *Uta*, *Urosaurus*, *Sator*, and *Sceloporus* demonstrating the absence of the scapular



IE—Intercostalis externi

SD—Serratus (dorsal part)

SP—Spinus dorsi

Fig. 8. Dorsal view of head and neck musculature; fourth depth at left and fifth depth at right. A. *Uta*; B. *Urosaurus*.

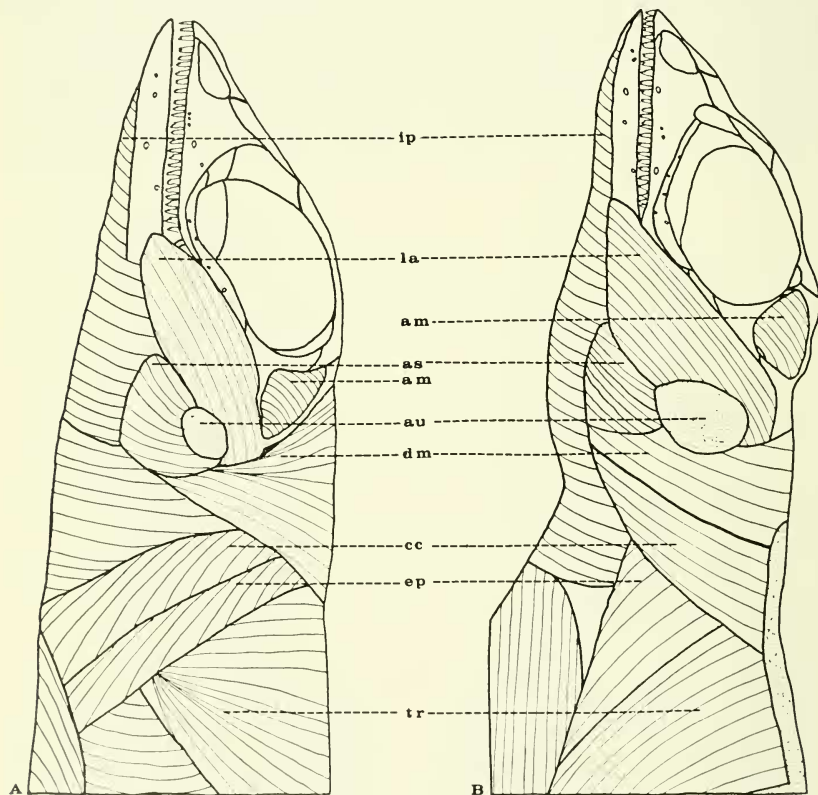
fenestra; and (3) *Petrosaurus* possessing very few osteological comparisons to the other sceloporines.

Presch (1969) reported that the osteological characteristics indicate that the horned lizards (*Phrynosoma*) form a highly specialized genus within the sceloporine group of genera. *Phrynosoma* is distinguished from all other members in having a large sternal fontanelle. *Petrosaurus*, he states, is clearly primitive with its moderately sized sternal fontanelle and four sternal ribs. Of the two groups derived from *Petrosaurus*, the least altered

are *Urosaurus*, *Uta*, *Sceloporus*, and *Sator*, with hooks on the clavicle and a covering over the anterolateral processes of the frontal. Thus Presch places *Uta* and *Urosaurus* in the same group but as distinct genera.

Zug (1971) studied arterial patterns in many iguanids and found differences between *Uta* and *Urosaurus*. In his Figures 10 and 15 he illustrates these differences. Particularly significant is the representation of separate phylogenetic lines for these genera.

Recently Purdue and Carpenter (1972)



AM—Adductor mandibularis
externus medius
AS—Adductor mandibularis
externus superficialis
AU—Auditory meatus

CC—Constrictor colli
DM—Depressor mandibularis
EP—Episternocleidomastoideus
IP—Intermandibularis
posterior

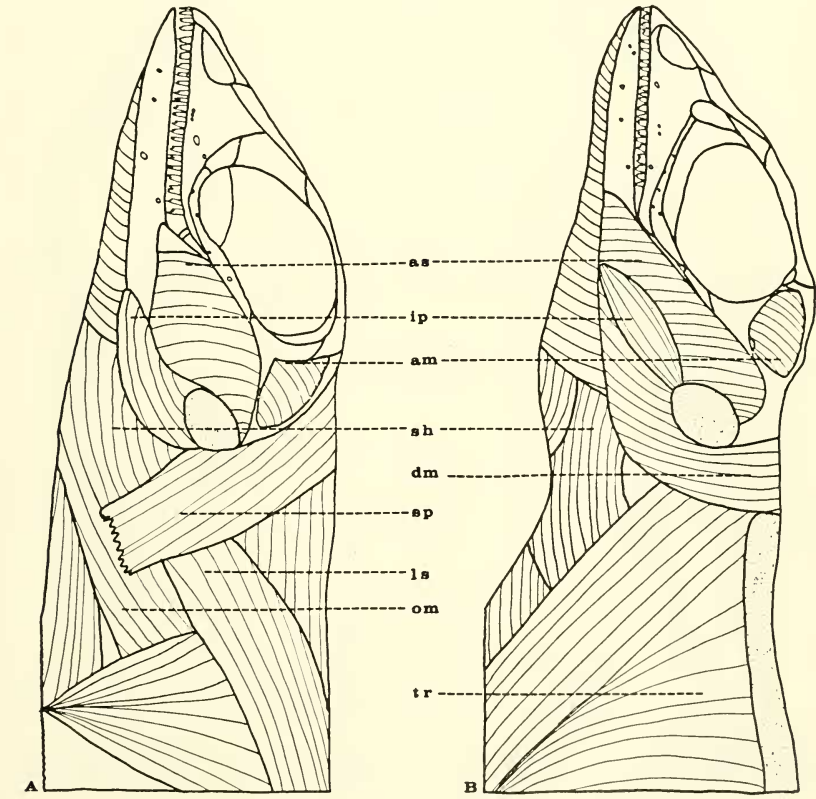
LA—Levator angularis
oris
TR—Trapezius

Fig. 9. Lateral view of head and neck musculature; superficial depth. A. *Uta*; B. *Urosaurus*.

have studied the relationships of *Sceloporus*, *Uta*, and *Urosaurus* as determined by their display motions and based on ratios of hip and shoulder movement to vertical eye movement. They suggest that *Uta* and *Urosaurus* are distinct genera and that *Urosaurus* is derived from one group of *Sceloporus*, while *Uta* is more closely related to *Petrosaurus*.

Larsen and Tanner (1975) have presented a new phylogeny for the sceloporines based on external characteristics including the development of specialized scales and structure of the gular fold, and

internal characters including hip and shoulder ratios. They indicate that *Sceloporus* is advanced and derived from one line of sceloporines, including *Sator*, *Urosaurus*, *Uta*, and *Petrosaurus*; while *Phrynosoma* and the sand lizards, including *Uma*, *Callisaurus*, *Holbrookia*, and *Cophosaurus*, comprise a separate line of evolution. They separate the primitive species of *Sceloporus* from that genus and resurrect Cope's genus *Lysioptychus* for them. They also consider *Uta* and *Urosaurus* to be closely related, with *Uta* being the more primitive.



- | | | |
|--|-----------------------------------|--------------------------------------|
| AM—Adductor mandibularis
externus medius | DM—Depressor mandibularis | LS—Levator scapulae
superficialis |
| AS—Adductor mandibularis
externus superficialis | EP—Episternocleidomastoideus | OM—Omohyoideus |
| | IP—Intermandibularis
posterior | SH—Sternohyoideus |

Fig. 10. Lateral view of head and neck musculature: first depth. A. *Uta*; B. *Urosaurus*.

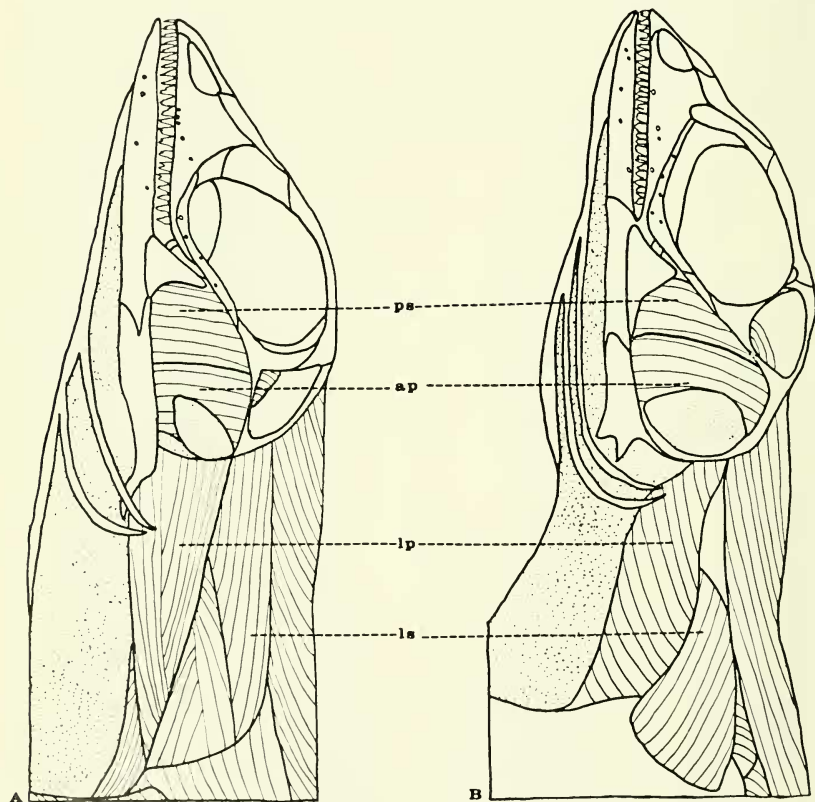
Osteology

As stated earlier, length-width measurements of bones and bone shapes were utilized to analyze the osteological relationships between the two genera. The ratio means in Tables 1 and 2 were used to make these relationships clear. Utilizing the method of Avery and Tanner (1971), one can assume that a difference of .40 or fewer percentage points (.20-.60) between means of the same bone indicates a close relationship. The possession of bones with similar shape is also an indicator of close relationship.

Based on comparisons of the skulls of iguane lizards, Avery and Tanner (1971) indicate osteological characters of the skulls of iguanid lizards to be stable within generic limits. This osteological stability is also demonstrated by the skulls of *Uta* and *Urosaurus*.

Reviewing Tables 1 and 2, the 35 characteristics and corresponding mean ratios indicate 24 structures with mean ratios differing by .40 or more percentage points (.20-.65).

As indicated by Etheridge (1964), the difference between the skull length and



AP—Adductor mandibularis
externus profundus
LP—Levator scapulae
profundus

LS—Levator scapulae
superficialis

PS—Pseudotemporalis
superficialis

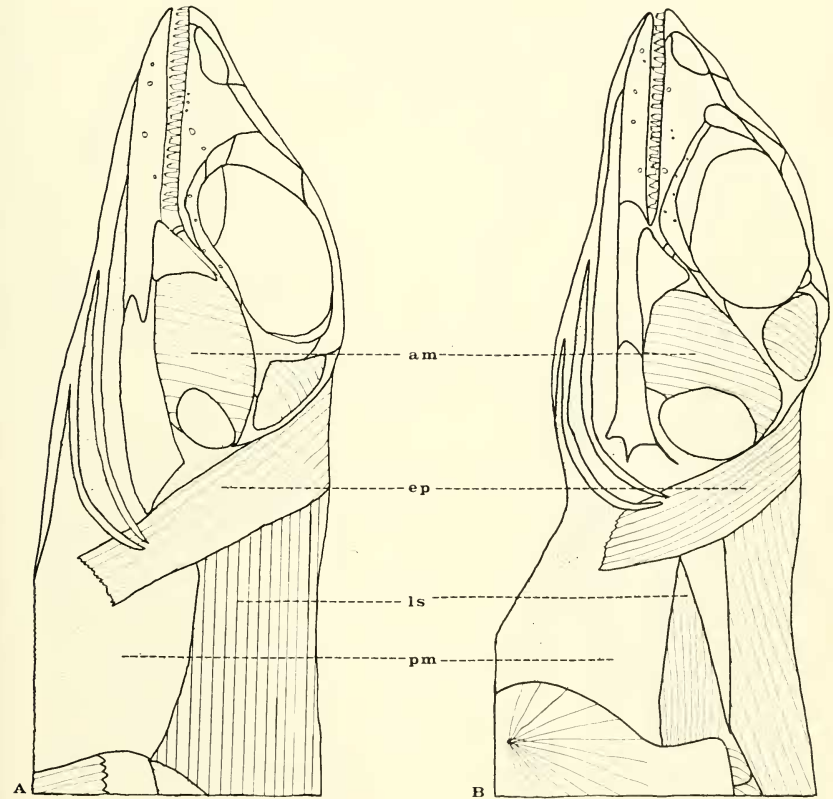
Fig. 11. Lateral view of head and neck musculature; second depth. A. *Uta*; B. *Urosaurus*.

width ratio in *Uta* and *Urosaurus* is almost negligible. However, our measurements of the basisphenoid and basioccipital bones show differences of 1.05 and 1.46 points respectively, along with the more posterior location of the suture between the two structures.

Considering the ventral bone structures (Fig. 1), the following mathematical differences exist. Both the pterygoid and ectopterygoid bones differ by more than .40 points (Tables 1 and 2); however, the ectopterygoid possessed by *Urosaurus* shows anterior wings extending to the maxilla, not seen in *Uta*. The primary

differences found between the vomer and palatine bones in both genera is mainly the positioning of their common suture. In *Urosaurus* the suture extends antero-medially from the inferior orbital foramen to the fenestra exochioanalis, whereas in *Uta* the suture is found extending laterally from the anterior portion of the pyriform recess to the maxilla.

In reference to the nasal capsule (nasal, prefrontal, lacrimal, and septomaxilla), there are found ratio differences in the nasal and lacrimal (slight difference in the prefrontal) and practically no structural peculiarities. The premaxilla and



AM—Adductor mandibularis
externus medius
EP—Episternocleidomastoideus

LS—Levator scapulae
superficialis

PM—Pharyngeal
membrane

Fig. 12. Lateral view of head and neck musculature; third depth. A. *Uta*; B. *Urosaurus*.

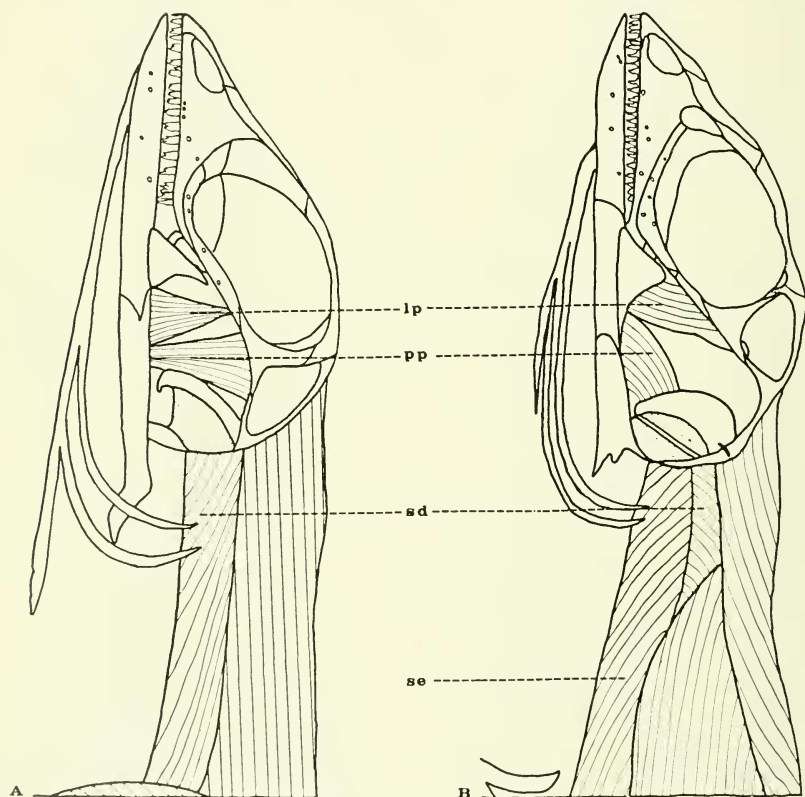
maxilla of the palate complex show a discrepancy only in the premaxilla. The premaxillary bones of the two genera differ by .77 points with the premaxilla of *Uta* being narrower anteriorly than in *Urosaurus*.

The parietal, squamosal, and quadrate (of the temporal fenestra portion of the maxillary segment) all differ in size, shape, and ratio. The parietal in *Uta* is much more rectangular and broad than in *Urosaurus* and covers more of the posterior portion of the braincase. The difference between the squamosal and quadrate

in both genera is mostly in ratio (shape-size) rather than in location.

On the dorsal area of the skull a striking difference is noticed in the size and shape of the fenestra exourina. In *Uta* the fenestra is oval and quite similar to that of *Sauromalus o. multiforaminatus* (Avery and Tanner, 1964), whereas in *Urosaurus* the anterior portion of the fenestra is expanded anterolaterally.

Turning to the mandible, we see several differences. The articular differs by 1.92 points in *Uta* and is only half the length seen in *Urosaurus*. The largest mandib-



AM—Adductor mandibularis
posterior
PP—Protractor pterygoideus

PT—Pseudotemporalis
profundus
SD—Spinus dorsi

SS—Suprascapula

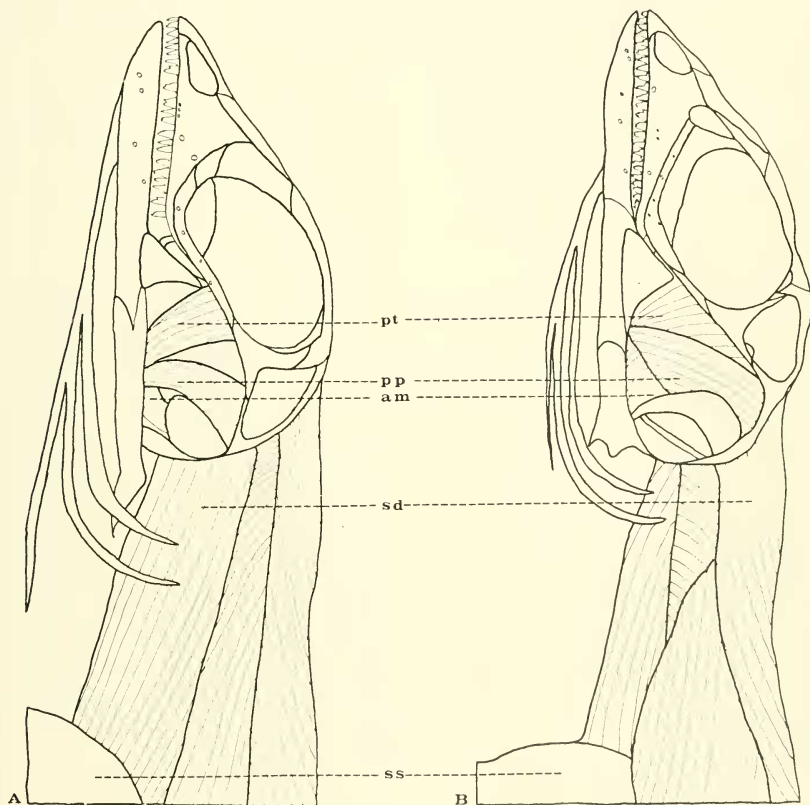
Fig. 13. Lateral depth of head and neck musculature; fourth depth. A. *Uta*; B. *Urosaurus*.

ular difference is in the size and location of the surangular, where the ratio differential is .86 points and the position in *Urosaurus* is directly ventral to the coronoid. In *Uta*, however, it is posteroventral to the coronoid with only an anterior wing making contact with the coronoid anteriorly. This arrangement of the surangular and coronoid found in *Uta* is similar to *Amblyrhynchus cristatus*, *Brachylophus fasciatus*, *Chalarodon madagascarensis*, *Conolophus pallidus*, *Ctenosaura pectinata*, *Cyclura macclayi*, *Dipsosaurus dorsalis*, *Iguana iguana*, *Oplurus sebac*, and *Sauromalus obesus* (Avery and Tan-

ner, 1971). None of these are similar to *Urosaurus*.

Myology

The anterior anatomy in *Uta* when compared with that in *Urosaurus* shows observable myological differences. In considering the M. omohyoideus, M. sternohyoideus, and M. sternothroideus, one can see that all three muscles were distinctly separated in *Uta* as they were reported for the iguanids *Cyclura nuchalis* and *Sauromalus obesus* by Avery and Tanner (1971), whereas *Urosaurus* resembles slightly that of *Brachylophus fasciatus*.



LP—Levator pterygoideus
PP—Protractor pterygoideus

SD—Spinus dors
SE—Serratus (dorsal part)

Fig. 14. Lateral view of head and neck musculature; fifth depth. A. *Uta*; B. *Urosaurus*.

The dorsal musculature at the first depth shows a distinct difference between *Uta* and *Urosaurus*. The M. levator scapulae superficialis, which is evident in all species studied by Avery and Tanner (1971) as well as in *Uta*, was overlaid by the trapezius complex in *Urosaurus*. Another distinction of the ventral musculature is that seen in the M. episternocleidomastoideus. In *Uta*, as in the genera studied by Avery and Tanner, the M. episternocleidomastoideus and the levator scapulae profundus are found anterior to the M. levator scapulae superficialis, whereas in *Urosaurus* the position of these two muscles is posterior to M. levator scapulae superficialis.

Lateral musculature shows some similarities between *Urosaurus*, *Chalarodon madagascarensis*, and *Oplurus schae*. While the similarity of *Uta* to *Sauromalus obesus* and *Cyclura nuchalis* (Avery and Tanner 1971) is noticeable. In *Urosaurus* the M. episternocleidomastoideus is overlaid by the trapezius, whereas in *Uta* it is not covered. The M. episternocleidomastoideus and M. levator scapulae superficialis of *Urosaurus* are buried beneath the second depth of muscle tissue, while in *Uta* these muscles are mostly superficial.

The orientation of the M. levator scapulae superficialis and M. levator scapulae profundus at the third depth is the same in *Urosaurus* and *Chalarodon madagascarensis*, while these muscles in *Uta* resemble *Sauromalus obesus* and *Cyclura nuchalis*. In *Urosaurus* the M. levator scapulae superficialis covers the M. levator scapulae profundus posteriorly as seen in *Chalarodon madagascarensis* (Avery and Tanner, 1971). In *Sauromalus obesus* the common border of the M. levator scapulae profundus and M. levator scapulae superficialis is similar to that in *Uta*.

The temporal musculature of *Cyclura nuchalis* (Avery and Tanner, 1971), M. protractor pterygoideus, M. pseudotemporalis profundus, and M. levator pterygoideus appears to be similar to that of *Uta*, whereas in *Urosaurus* these muscles are seemingly very similar to those of *Chalarodon*.

Phylogenetic Relationships

Larsen and Tanner (1975) consider *Uta* to be more primitive than *Urosaurus* and both more primitive than *Sceloporus*.

based on internal and external characters. We agree with this analysis of *Uta's* relationship to *Urosaurus*. We believe that *Uta* is more primitive for the following reasons: 1. The ectopterygoid of *Uta* is simple in structure and shape, while that of *Urosaurus* is greatly expanded and more complex in shape. 2. The fenestra exaraina of *Uta* is similar to that of *Sauromalus*, a primitive iguanine lizard. 3. The structure of the surangular and coronoid bones in *Uta* is similar to that seen in the more primitive iguanines and the Madagascar iguanids. 4. The omohyoideus muscle complex in *Uta* may be subdivided into three distinct muscle bundles as seen in the primitive *Cyclura* and *Sauromalus*, whereas *Urosaurus* resembles the omohyoideus configuration seen in the specialized *Brachylophus*. 5. In *Uta* the levator scapulae superficialis, levator scapulae profundus, and the episternocleidomastoideus muscles have a configuration similar to the more primitive iguanines. In *Urosaurus* the muscle pattern shows considerable deviation. 6. In *Uta* the levator scapulae superficialis is superficial while it is overlain by the trapezius complex in *Urosaurus*, indicating to us a higher degree of specialization.

The similarity of these two genera to the Madagascar iguanids *Chalarodon* and *Oplurus* remains a confused question. If *Oplurus* is ancestral to the iguanine lizards as indicated by Avery and Tanner (1971), is *Chalarodon* also ancestral to the sceloporine lizards? Apparently not since both *Uta* and *Urosaurus* share some characteristics with *Chalarodon* and *Oplurus* without establishing a consistent pattern of relationship. These similarities are more likely the result of parallelism than a close phylogenetic relationship. All four genera are desert animals and *Chalarodon* superficially resembles both *Uta* and *Urosaurus* externally.

Perhaps future comparisons should be made between *Phrynosoma* and *Petrosaurus* and the Madagascar iguanids to determine the phylogenies of the main lines of iguanid evolution and the Madagascar iguanids.

CONCLUSIONS AND SUMMARY

Data derived from the preceding observations strongly indicate that *Uta* and *Urosaurus* are distinct genera. These con-

clusions are based on the distinct osteological and myological characteristics found in the head and throat anatomy.

Osteological differences are summarized as follows: 1. Bones showing major differences in size and shape are the basi-sphenoid, basioccipital, pterygoid, ectopterygoid, premaxilla, articular, and surangular. 2. The ectopterygoid possesses an extended anterior wing to the maxilla in *Urosaurus* which is not present in *Uta*. 3. The parietal in *Uta* is much more rectangular and broader than in *Urosaurus*. 4. The fenestra exonarina in *Uta* is oval, whereas in *Urosaurus* the anterior portion is expanded anterolaterally. 5. The position of the surangular in *Urosaurus* is directly ventral to the coronoid, but in *Uta* it is posteroventral to the coronoid with only an anterior wing making a narrow contact with the coronoid.

Several noticeable generic myological differences are apparent: 1. A distinct separation of the M. omohyoideus, M. sternohyoideus, and M. sternothyroideus is seen in *Uta*, whereas in *Urosaurus* only the M. omohyoideus and M. sternohyoideus are discernible. 2. The M. levator scapulae superficialis at the first depth is superficial in *Uta* but is overlain by the trapezius complex in *Urosaurus*. 3. In *Uta* the M. episternocleidomastoideus and the M. levator scapulae profundus are anterior to the M. levator scapulae superficialis, whereas in *Urosaurus* the position of the first two muscles is posterior to the latter muscle. 4. The M. protractor pterygoideus, M. pseudotemporalis profundus, and M. levator pterygoideus of *Uta* are similar to those of *Cyclura nuchalis*, while in *Urosaurus* these muscles are similar to *Chalarodon*.

Because *Uta* and *Urosaurus* exhibit such distinct anatomical differences, the separate generic designations assigned to them are considered to be valid. Phylogenetically *Uta* is considered to be older and more primitive than *Urosaurus* because of (1) the simple structure of the ectopterygoid in *Uta*, (2) the primitive shape of the fenestra exonarina, (3) the common arrangement of the surangular and coronoid bones in *Uta*, (4) the common arrangement of the M. omohyoideus complex in *Uta* and the primitive iguanines, and (5) the common configuration of the posterior skull and anterior shoulder mus-

culation of *Uta* and the primitive iguanines.

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